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Interspecific aggression declines seasonally in breeding great tits *Parus major*

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Abstract

During the breeding season, great tits show aggression to protect their nest from intra- and interspecific intruders. Aggression is a labile trait that can be plastically expressed as a result of individual differences (e.g., personality), seasonal gradients in the costs and benefits of aggression, or other environmental components (e.g., number of competitors). Competitors may try to take over great tit nests, because the number of suitable nesting sites is limited, and great tits may guard high quality territories. Taking over a great tit nest may be especially fruitful in early phenological stages (egg laying) when great tits frequent their nests less often. However, great tits may compensate for this vulnerability by being more aggressive toward intruders during early nesting stages, a pattern that has already been established in an intraspecific context. Previous studies have shown that interspecific intruders were most likely to die from great tit aggression during great tit egg laying, suggesting great tits may also be more aggressive during this phase in an interspecific context. Here, I tested this hypothesis with simulated territorial intrusions in great tit territories using taxidermized blue tits *Cyanistes caeruleus* (hereafter called blue tit models). Great tit aggression (number of calls and approach distance toward blue tit model) was assayed during egg laying, incubation, and chick rearing in the breeding season of 2014. Although sample size was low due to a high fraction of non-responders ($n = 44$ out of 89 assays across 26 out of 35 individuals), I found that great tits showed a seasonal decline in aggressiveness, which is congruent with intraspecific results on this study species. I discuss my findings in the context of differential adjustment to climate change between interspecific competitors.

KEYWORDS

aggression, interspecific competition, personality, phenology, simulated intrusion, territory

1 | INTRODUCTION

During the breeding season, great tits are territorial to defend their nest from intruders (Krebs, 1971, 1982). Aggression is one of the manifestations of territoriality, the level of which can differ among individuals (i.e., personality) or across contexts (Araya-Ajoy &

Dingemanse, 2014, 2017). Interspecific intruders may prospect at great tit breeding sites to look for high quality nesting sites (Forsman & Thomson, 2008; Jaakkonen, Kivelä, Meier, & Forsman, 2015; Samplonius, Van Der Meer, & Both, 2017), which can have negative fitness consequences for the tits if prospectors settle nearby (Forsman, Thomson, & Seppänen, 2007). Prospectors may even be

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killed by breeding great tits in attempting to take over their nest (Ahola, Laaksonen, Eeva, & Lehikoinen, 2007; Merilä & Wiggins, 1995; Slagsvold, 1975). Such dramatic end games have mainly been observed between great tits and pied (*Ficedula hypoleuca*) and collared flycatchers (*Ficedula albicollis*). The probability of being killed by tits is associated with the phenological phase of the great tit with more victims during the egg-laying phase of great tits (Ahola et al., 2007; Merilä & Wiggins, 1995). The occurrence of flycatcher victims may partly be due to great tits frequenting their nests less often during egg laying than during later breeding phases, combined with the flycatcher arrival peak potentially coinciding with great tit egg laying (here called the coincidence hypothesis). Testing the coincidence hypothesis would require detailed observations of nest box visitation rates of both great tits and interspecific prospectors during different phenological phases across multiple years, which was not the focus of this study.

In addition to the coincidence hypothesis, the occurrence of flycatcher victims may partly be due to great tits being principally more aggressive during egg laying (here called the aggression hypothesis). The two hypotheses are not mutually exclusive, but could enhance each other's effects. Interestingly, great tit aggression is a labile trait that generally is higher during egg laying than during incubation in an intraspecific context Araya-Ajoy & Dingemanse, 2014; Araya-Ajoy & Dingemanse, 2017). It is interesting to study the same patterns in an interspecific context (both in the case of the coincidence and the aggression hypothesis), because climate change can differentially affect the phenology of interspecific competitors (Phillimore, Leech, Pearce-Higgins, & Hadfield, 2016; Samplonius et al., 2018) and the overlap in their distributions (Carter, Saenz, & Rudolf, 2018; Usui, Butchart, & Phillimore, 2017). Therefore, the scope of interspecific conflict may be altered by climate change (Ahola et al., 2007). Here, I tested whether great tits show variable aggression across different phenological phases, using a common interspecific competitor, the blue tit, as a model. Ideally, I would have preferred to use pied flycatchers, but these were impossible to obtain. However, interspecific interference competition has been extensively described between great tits and blue tits as well (Barrientos, Bueno-Enciso, Serrano-Davies, & Sanz, 2015; Dhondt & Adriaensen, 1999; Minot & Perrins, 1986), justifying the use of a blue tit model. My main expectation was that great tits become less aggressive toward interspecific intruders over the course of the breeding season.

2 | MATERIALS AND METHODS

2.1 | Study site

Simulated territorial intrusions were performed in the Netherlands in National park Dwingelderveld in two subareas (Dwingelderveld 52°49'05"N 6°25'46"E and Lheebroek 52°50'14"N 6°26'45"E), each with 100 nest boxes from April to June 2014. Nest boxes in these populations are attached to trees at about 1.5 m from the ground. The areas are structurally dominated by oak (*Quercus robur* and *Quercus petraea*), birch (*Betula* spp), and beech (*Fagus sylvatica*). The

main occupants of the nest boxes were great tits ($n = 64$), pied flycatchers ($n = 49$), and blue tits ($n = 22$). These areas did not differ in the number of tits, but Lheebroek had slightly lower densities of pied flycatchers ($n = 19$) and more unoccupied nest boxes ($n = 38$ instead of $n = 22$ in Dwingelderveld). Data on egg-laying timing, clutch size, and hatching date were collected during full plot checks every five days. The most intense monitoring of this population is for pied flycatchers, which are also ringed and scored for arrival date daily. More details on general field protocols and study sites are available (Both, Bijlsma, & Ouweland, 2016; Both et al., 2017; Samplonius & Both, 2014).

2.2 | Simulated territorial intrusions

Three observers performed 89 simulated territorial intrusions (aggression tests) across 35 individuals between 7:30 and 15:00 hr, 44 of which elicited a response across 26 individuals. I adopted and slightly adjusted a protocol that was previously used in great tits (Araya-Ajoy & Dingemanse, 2014). To elicit an aggressive response from great tit occupants, one of four randomly selected blue tit models was presented on top of the great tit nest box during egg laying, incubation, and chick rearing. The blue tit models were protected by a thin, dark-green wire mesh cage with opening holes of 1×1 cm to prevent damage by defending great tits. A playback device (Radioshack mini amplifier 277–1,008°C) was set down next to it playing one of four randomly selected blue tit songs (recorded from Dutch populations). The volume of the device was set so that it sounded realistic to the human observer, but I have no data on the exact amplitude. The observer then positioned themselves at 25 m away from the nest box and hid at a spot where the great tit behavior could be observed. Observers were trained by the author to make sure everyone recorded data the same way.

Each assay lasted five minutes, and started as soon as a great tit male was within an estimated 10 m radius from the nest box. During the assay, the number of calls, the minimal approach distance of the great tit male to the blue tit model, the number of songs, and the number of attacks were monitored and estimated. If the great tit male landed on the cage (four cases), the minimal approach distance was recorded as 0.1 m. In other cases, the minimal distance was estimated after the assay by walking to the branch the bird sat on when it was closest to the blue tit model during the assay, and using the armspan of the observer to measure the distance between the blue tit model and that branch. Since all observers knew their own armspan, this method gave a decent estimate of the minimal distance. Although there may be some measurement error involved with this method, I did not expect this to be confounding for the analysis, since the variation in minimal distance was much larger than the potential measurement error. If there was no great tit response within a radius of 10 m from the nest box within 15 min of the blue tit model presentation, the assay was aborted. None of the great tits were seen attacking the blue tit, possibly because it was too well protected by the cage, so the number of attacks was zero for all assays and could therefore not be analyzed. Similarly, hardly any of the

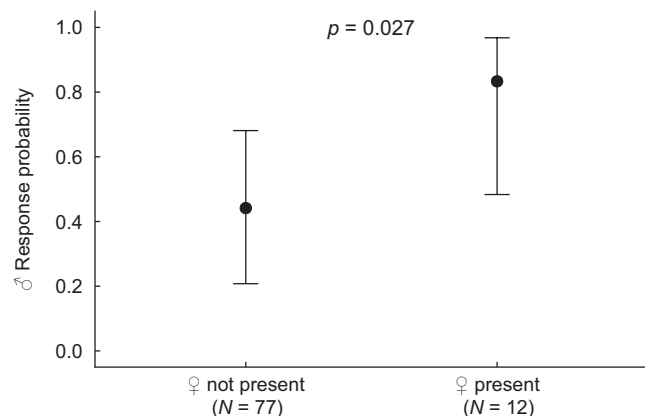


FIGURE 1 Males were more likely to respond to an aggression test when a female was present (Table 1). Female presence was included as a covariate in the models. Error bars represent 95% confidence intervals

great tits sang during the assay, so I also excluded songs from further analysis. However, previous research shows that the number of calls, the additive inverse of the minimal approach distance, and the number of attacks are all strongly correlated and part of the same latent variable, aggression (Araya-Ajoy & Dingemanse, 2014), so I assume that our two measures that showed considerable variation (calls and minimal distance) capture aggression well and allows for tentative inference about great tit propensity to attack. The males were focused on, because females typically kept more distance or went into the nest box during the assay. Unfortunately, blinded assays could not be done, because the observers were heavily involved in field work, and were therefore always intuitively aware which breeding stage the great tit was in.

2.3 | Statistical analyses

I used a binomial generalized linear mixed effect model (GLMM) to test whether the probability to respond to the assay changed across the breeding season (relative timing), and used two covariates: female presence (because males might be more likely to respond or be more aggressive when a female is present), and “study area.” Of the great tits that did respond to the test, I used linear mixed effect models (LMM, using Satterthwaite approximation to estimate the degrees of freedom) to test whether the number of calls and the minimal approach distance to the blue tit model changed across the breeding season. Since number of calls was a count variable, I square root transformed this variable to conform to the normal distribution (Figure S1). For the other response variables, the normal distribution was a reasonable assumption (Figures S2 and S3). The linear fixed effects used in all models were “relative timing,” “female presence,” and “area,” whereas “individual,” “sequence (4 levels),” and “observer (3 levels)” were used as a crossed random intercept to control for personality, habituation to the assay and observer effects. Sequence was not included as a fixed effect due to its high collinearity with relative date (VIF = 6.85). I subsequently performed

TABLE 1 Probability of great tits to respond to the simulated territorial intrusion was associated with female presence

	Probability to respond (SE)	
(Intercept, area DWL)	−0.290 (0.535)	$p = 0.59$
Relative timing	0.0080 (0.023)	$p = 0.72$
Female presence	1.961 (0.886)	$p = 0.027$
Area LBZ	0.079 (0.478)	$p = 0.87$

Values in bold are statistically significant.

a principal component analysis (PCA) on the two measured components of aggression (square root transformed number of calls and minimal approach distance to the blue tit models) and used the additive inverse of the eigenvalues of PC1 (calls and minimal distance were negatively correlated, so using the additive inverse allows for ease of interpretation: higher values now mean higher aggression) in a third model with the same predictors as in the other LMMs. In short, the following response variables were tested: probability to respond (GLMM, $n = 89$), square root number of calls (LMM, $n = 44$), minimal approach distance (LMM, $n = 42$), and -PC1 of calls and

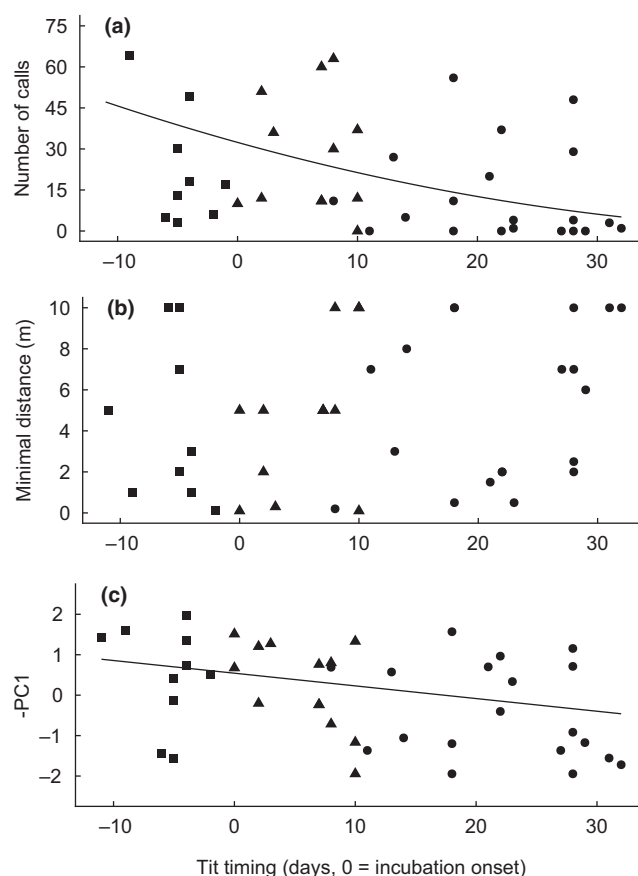


FIGURE 2 Great tit aggression throughout the breeding season (Table 2). The number of calls during the simulated intrusion declined (a), whereas the approach distance did not increase seasonally (b). Overall aggression decreased (c: eigenvalues of the first principal component = composite measure of (a) and (b)). Squares: egg-laying phase; triangles: incubation; circles: chick rearing

TABLE 2 Model outputs of linear mixed effect models testing the number of calls, minimal distance and a composite measure (PC1 of $\sqrt{\text{calls}}$ and distance) of great tits during simulated territorial intrusions

	$\sqrt{\text{calls}}$ (SE)		Minimal distance (SE)		-PC1 (SE)	
(Intercept, area DWL)	4.665 (0.809)	$p < 0.001$	5.372 (1.11)	$p = 0.011$	0.012 (0.320)	$p = 0.97$
Relative timing	-0.107 (0.034)	$p = 0.003$	0.044 (0.051)	$p = 0.45$	-0.031 (0.013)	$p = 0.025$
Female presence	1.50 (1.01)	$p = 0.14$	-2.296 (1.31)	$p = 0.088$	0.759 (0.402)	$p = 0.067$
Area LBZ	0.511 (0.928)	$p = 0.59$	-1.106 (1.111)	$p = 0.33$	0.305 (0.367)	$p = 0.42$

Values in bold are statistically significant.

distance (LMM, $n = 42$). In two instances, the observer had forgotten to write down the minimal approach distance, hence the lower sample size for that parameter. All analyses were performed in R 3.3.1 (R Development Core Team, 2016), using the package lme4 (Bates, Mächler, Bolker, & Walker, 2015).

3 | RESULTS

Male probability to respond to the test was higher when a female was present ($p = 0.027$, Figure 1, Tables 1, S1), but was unrelated to relative timing, making it unlikely that early and late aggression tests were from unique subsets of animals with differing personalities. Great tit males became less aggressive toward blue tit models as the breeding season progressed, with the highest aggression during the egg-laying phase. The number of calls toward the blue tit model declined seasonally ($p = 0.003$, Figure 2a, Tables 2, S1), but the approach distance did not change seasonally ($p = 0.45$, Figure 2b, Tables 2, S1), although this could be due to our low sample size ($n = 42$ assays across 26 individuals). The trend was in the expected direction (larger distance during later phenological phases). A principal component analysis on the two variables revealed that 71.5% of variation in aggression was explained by PC1, and the additive inverse of the eigenvalues of PC1 (latent variable "aggression") declined seasonally ($p = 0.025$, Figure 2c, Tables 2, S1).

4 | DISCUSSION

Great tit aggression toward simulated interspecific intruders declined seasonally. However, inference about this result should be taken with caution, as it is based on the subset of individuals that did respond to the assay. Although the sample size of this study was rather low, this result is in concurrence with previous studies on simulated territorial intrusions in great tits in an intraspecific context, which also found that great tit aggression decreased from egg laying to incubation (Araya-Ajoy & Dingemanse, 2014, 2017), and that the number of calls and the approach distance were highly correlated (i.e., great tits that called more were more likely to get closer to the blue tit model). I suggest that the apparently higher interspecific mortality during great tit egg laying reported in previous studies (Ahola et al., 2007; Merilä & Wiggins, 1995) could partly be due to

a higher great tit aggression during this phase and not just due to a higher chance of coincidental encounters.

These results are interesting in the light of ongoing climate change, which differentially alters the phenology and distribution of interspecific competitors (Carter et al., 2018; Phillimore et al., 2016; Samplonius et al., 2018; Usui et al., 2017). It is generally shown that resident species are more plastic in their response to temperature than migrants (Phillimore et al., 2016; Samplonius et al., 2018), causing their breeding phenologies to diverge. Such differential divergence has been shown to affect information use (Samplonius & Both, 2017), and here I show it could affect competitive interactions. This could mean that arriving competitors will encounter fewer aggressive great tits as climate change continues, because great tits advance their breeding phenology more than later breeding migrants in response to temperature (Samplonius et al., 2018).

It remains uncertain whether the number of prospectors increases aggression in great tits. If aggression is affected by the number of prospectors, then it would not matter how relative phenologies of interspecific competitors change, because tits would always be at their most aggressive when most prospectors are around. However, previous research shows that great tits are also most aggressive during egg laying in an intraspecific context in populations where hardly any other species breed in the nest boxes (Araya-Ajoy & Dingemanse, 2014, 2017). This implies that elevated aggression during egg laying is unrelated to the number of prospectors, but has more to do with the fertile period of the female and mate guarding (Björklund & Westman, 1986). Similarly, it is well known that for many animals testosterone levels are higher during periods of territory formation and mating, and lower during periods of parental care (Wingfield, Hegner, Dufty, & Ball, 1990). To disentangle the relative role of each of these factors, future studies could focus on how interspecific overlap in phenology alters aggression patterns, repeated over several years.

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SUPPORTING INFORMATION

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